Autecology of Successional Dominants of the Cool-temperate Forest in Japan : On Sapling Stage of Fagus crenata Blume

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Autecology of Successional Dominants of the Cool-temperate Forest in Japan : On Sapling Stage of *Fagus crenata* BLUME*

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Synopsis

Saplings of *Fagus crenata*, whose averaged height and weight were 124.1 cm and 237.3 g were grown at an experimental field located in the montane region of central Japan. The saplings initiated the leaf unfolding in mid May and shed the leaves in late October (about 150 leaf days) in 1989. The mean net increment of the plant was 156.6 g during the growing season. The current shoots and leaves were formed from the reserve matter produced and stored in the branches and trunk during previous year. The relationship between weight masses of above- (T : g) and below (R : g) ground was described as: $R=0.77T^{1.18}$. The relationship between weight masses of leaves (Wl : g) and trunk and branches (Wtb : g) is given as: $Wtb=3.75Wl^{1.07}$. The weight ratio of leaves to whole plant was about 12% through the growing season.

The plant absorbed 910 mg of nitrogen from the soil during April to September. The nitrogen was first allocated to leaves and re-allocated from the leaves to the branches and trunk at shedding. The weight ratio of plant net increment to total nitrogen absorbed from soil was 172.1. By combining these ecological characteristics, *Fagus crenata* appeared to be dominant in the climax forest.

Key words: *Fagus crenata*, allometry, nitrogen allocation, T/R ratio

Introduction

This paper describes ecological characteristics of *Fagus crenata* BLUME, a dominant of the

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climax forest in the cool-temperate region of Japan. We have studied the ecological characteristics of *Fagus crenata*, in order to learn the type of life history of this species. The type of life history was defined as a particular combination of ecological characteristics for reproduction or for perpetuation of the species (HAYASHI 1977). The following ecological characteristics were recorded: tree height, diameter at stem base, plant weight, weight ratio of above- and below ground parts of plant, weight ratio of leaf mass: branch and trunk masses. The seasonal change in nitrogen and carbon content of each plant organ was also determined.

Previous ecological and phytosociological studies on *Fagus crenata* forests have been carried out by many authors (YOSHIOKA 1952, NOMOTO 1964, SASAKI 1970, YAMAMOTO 1989, HUKUSIMA *et al.* 1995). Flowering and seed production of *Fagus crenata* population were studied by HASHIZUME and HUKUTOMI (1978). Reproductive organs for a forest stand of this species were measured by SAITO *et al.* (1991). Seedling populations in the *Fagus crenata* stand were studied by HARA (1987) and HASHIZUME and NOGUCHI (1977). NAKASHIZUKA and NUMATA (1982) worked on the regeneration and maintenance of *Fagus crenata* forest. NAKASHIZUKA (1988) reported recruitment and survivorship of *Fagus crenata* seedlings under a natural forest with dwarf bamboo in the floor. MARUYAMA and KAZAMA (1987) conducted experiments on photosynthesis of *Fagus crenata* seedlings. PETERS and POULSON (1994) reported stem growth and canopy dynamics of *Fagus* forests. The present paper is an initial step to find out how does the type of life history of this species contribute to predominate at the stage of climax.

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Materials and Methods

Saplings of *Fagus crenata* were studied for plants in a experimental field in the campus of Sugadaira Montane Research Center, University of Tsukuba (SMRCT) (36°31' N and 138°21' E). Mean annual temperature and total precipitation during the experimental year were 7.8°C and 1,568 mm, respectively. KIRA's warmth and coldness indices are 62.0 and -27.9°C month (KIRA 1945). The soils were derived from volcanic ash; the soil characteristics were pH 4.5, 13.9% organic carbon and 0.75% nitrogen.

Forty nine plants in varying sizes were adopted for measuring the ecological characteristics of this species. Twenty five saplings out of these plants averaging 9 years old, 124.1 cm in mean height and 237.3 g in mean dry weight were used for the growth experiment. After measuring the plant height and diameter at stem base, the saplings were planted in center of a 2×2 m grid and left to grow under natural conditions. The experimental period was from 7th April 1989 to 25th November 1989. Five saplings were harvested at random from the experimental field on following dates in 1989: 2nd May (just before leaf unfolding), 8th June (when all leaves had reached maximum size), 6th August (maximum assimilation appeared to have occurred), 28th September (10% of the leaves had changed to yellow), 23rd October (all

the leaves had changed to yellow). The materials collected on 25th November (winter bud had formed) were used for carbon and nitrogen analysis only. The rest of the plants were used for measurement of quantitative aspect of growth form of plants in varying seasons.

After washing in tap water, the plants were dissected into bud, leaf, shoot, branch, trunk, main root and rootlet. Measurement of withered roots during the experiment was impossible. The organs were weighed after drying in an oven at 85°C. In order to obtain dry weight, the trunks were kept in the oven for 132 hr, main roots for 120 hr, branches for 30 hr and the leaves, bud and rootlet for 6 hr. Measurement of leaf area was made on 28th September 1989. Nitrogen and carbon concentrations for each organ were determined at each sampling using a carbon and nitrogen analyzer (Yanagimoto MT500). The nitrogen and carbon content of each organ was obtained by multiplying the nitrogen concentration and mass of each organ.

The solar radiation was measured in the SMRCT during the experimental year and the radiation time was determined as the duration that the short wave radiation was recorded.

Results

Phenology

Leaf unfolding of the saplings was initiated on 21st May, when the warmth index was 158°C • day, and the leaf attained maximum size on 6th June. Sixteen days with a 3.7 standard deviation were needed for leaf unfolding. Plants maintained the leaves throughout the summer without any shedding; about 10% of leaves changed to yellow on 30th September. The leaf period was 150 days, if we regard the final day as when 50% of leaves changed to yellow.

Allometry and estimation of plant weight

The relationship between plant weight (W : g) and product of plant height (H : cm) and square diameter at stem base (D^2H : cm, cm) is shown in Fig. 1. The relationship is given as:

$$W = 0.91\ (D^2H)^{0.88} \qquad r = 0.98 \quad \cdots\cdots\cdots\cdots \quad (1)$$

The constants of the relationship, however, varied according to the season, as shown in Table 1. The weight of individual plant in April was estimated using the constants of April in Table 1. The average weight and height of 25 plants in April were estimated as 237.3 g,

Table 1. The constants of allometric relationships between plant weight (W : g) and product (D^2H) of square diameter (D^2 : cm) and plant height (H : cm) in different seasons. Relationship is described as $W = a\ (D^2H)^b$.

Date of harvest	a	b	Correlation coefficient
7 Apr.	0.66	0.92	0.96
8 Jun.	0.25	1.04	0.99
6 Aug.- 23 Oct.	0.91	0.88	0.98

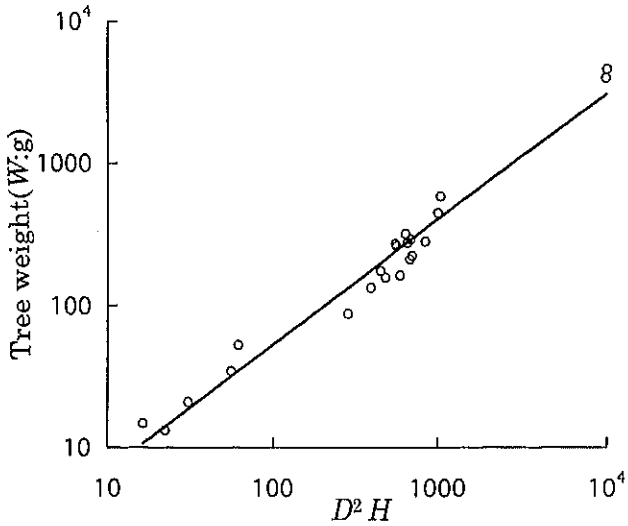

Fig. 1. Relationship between plant weight (W : g) and product of square diameter at stem base and plant height (D^2H : cm, cm).

and 124.1 cm and are referred as the "plant weight" and "plant height" (averaged plant weight and plant height in this experiment). The weight increment was obtained as the difference between measured value at harvest and estimated value of the same plants in April. The growth ratio in this paper was used as the ratio of plant weight in April to that at harvest. The plant weight growth at each harvest was obtained as the product of average plant weight (237.3 g) in April and growth ratio at each harvest. For example, mean weight of the plants

Table 2. Measured weight at harvest (a : g) and estimated weight in April (b : g) of the same plants. The growth of the plant is product to mean weight of plant in April (237.3 g) and growth ratio.

Date of harvest	Measured plant weight at each harvest (a) [mean (SD)]	Estimated plant weight in April (b) [mean (SD)]	Growth (a)-(b)	Growth ratio (c) (a) : (b)	Growth of plant [237.3×(c)]	Net assimilation	Duration (days)
7 Apr.	—	237.3(137.4)	0	—	237.3	0	0
2 May	234.9 (58.8)	243.8 (82.7)	-8.9	0.96	227.8	-9.5	25
8 Jun.	182.1 (72.4)	186.3 (62.8)	-4.2	0.97	230.0	2.2	37
6 Aug.	285.7(111.1)	187.5 (62.8)	98.2	1.52	360.6	130.6	59
28 Sep.	314.9(161.2)	189.5(64.6)	125.4	1.66	393.9	33.3	53
23 Oct.	478.9(285.6)	309.6(148.1)	169.3	1.55	367.8	-26.1	25

SD: standard deviation.

harvested in September was 314.9 g and the estimated weight of the same plants in April was 189.5 g (Table 2). Therefore, the weight growth from April to September was 125.4 g. The growth ratio was 1.66 which was obtained as a ratio of the weight in April (189.5 g) to the weight in September (314.9 g). In other words, the plants increased weight 1.66 times from April to September. Using this value we are able to estimate weight increment of 156.6 g and a September plant phytomass of 393.9 g (237.3 g in April).

Plant growth

The plant growth weight is shown in Table 2. The weight decreased from 237.3 g to 227.8 g during the period from 7th April to 2nd May. The phytomass then increased continuously to 393.9 g on 28th September. Net increment of phytomass was 156.6 g per 174 days. The maximum increment was observed during the period 8th June to 6th August, which was 83% of the total increment for the growing season. The plant weight decreased from 393.9 g to 367.8 g (6.6% of total weight) from 28th September to 23rd October as a result of leaf shedding and respiration. The plant height increased from 124.1 cm on 21st May to 152.9 cm on 6th June. The height growth was 28.8 cm, with standard deviation of 7.1 cm, with a growth rate of 1.8 cm/day. The 1 g of leaves was equivalent to 184.3 cm^2 in leaf area on 28th September. The figure was smaller than that obtained by YAMAMURA *et al.* (1993) as 293 cm^2. This may due to difference of habitats where the saplings were collected. YAMAMURA *et al.* (1993) collected the saplings from inside forest and ours were grown in the experimental field.

Quantitative aspects of the plant

The relationship between above- (T : g) and below ground (R : g) parts is given in Fig. 2

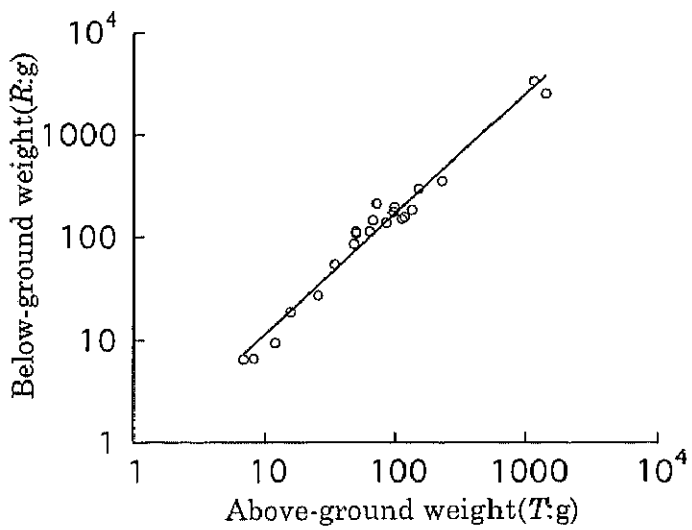

Fig. 2. Relationship between weights of above- (T : g) and below ground (R : g) parts.

for 22 plants of varying sizes. The relationship is described as:

$$R=0.77T^{1.18} \qquad r=0.99 \quad \cdots\cdots\cdots\cdots \quad (2)$$

The constants for the equation are applicable to the plants in seasons both with and without leaves except for plants just after leaf unfolding. The values for plants just after leaf unfolding are coefficient of 0.81 at a power of 0.88. The weight ratio of rootlet to main root was 0.24 with standard deviation of 0.13. The relationship between weights of trunks and branches (Wtb: g) and leaf (Wl: g) is given in Fig. 3. This relationship is described as:

$$Wtb=3.75\,Wl^{1.07} \qquad r=0.88 \quad \cdots\cdots\cdots\cdots \quad (3)$$

This equation is applicable to all plants for all seasons.

The average weight ratio of trunk plus branches to leaves was 4.86 with a standard deviation of 1.78. The relationship between leaf mass (Wl) and square diameter of stem base and plant height (D^2H) is given in Fig. 4. The relation is described as:

$$Wl=0.1\,(D^2H)^{0.88} \qquad r=0.93 \quad \cdots\cdots\cdots\cdots \quad (4)$$

Using equation (4), we can estimate total leaf area of a sapling by multiplying the Wl and 184.3 cm². Therefore, the total leaf area of this plant in August was 8,176.7 cm².

Seasonal change of weight ratio of each organ to whole plant

The seasonal change of weight ratio of each organ to whole plant is given in Fig. 5. The weight ratio of organs to whole plant in early August (just after leaf unfolding was completed) was 12% in leaf (Wl/W) 17% in branch (Wb/W), 3% in current shoot, 35% in trunk (Wt/W), 6% in rootlet (Rl/W) and 30% in main root (Rm/W). The weight ratio of buds (Wbd/W) for plant was 2% before leaf unfolding, they then grew to form new shoots and leaves. In November, the next year's buds were formed. After 8th June the Wl/W was constant at

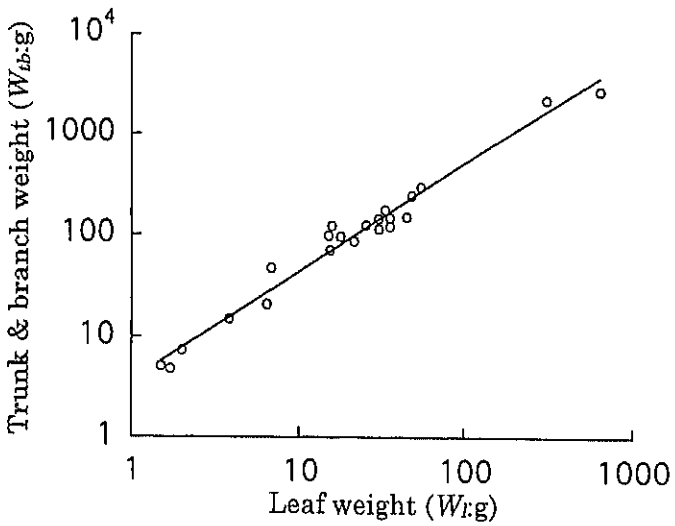

Fig. 3. Relationship between weights of leaves (Wl: g), branches and trunk (Wtb: g).

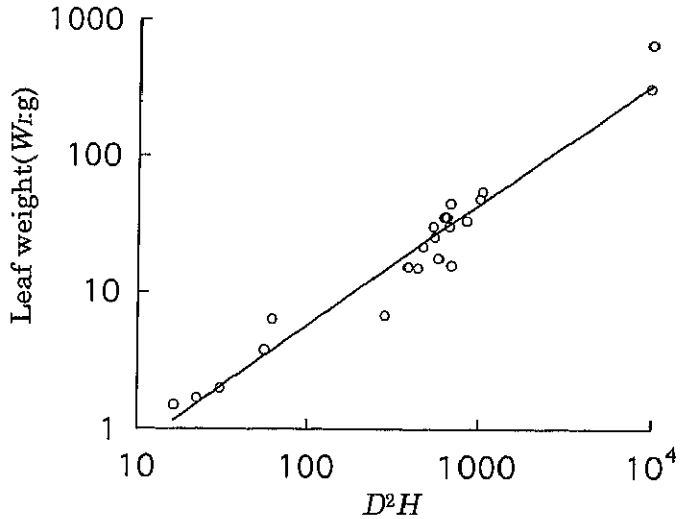

Fig. 4. Relationship between leaf mass (*Wl* : g) and product of square diameter at stem base and tree height (D^2H : cm, cm).

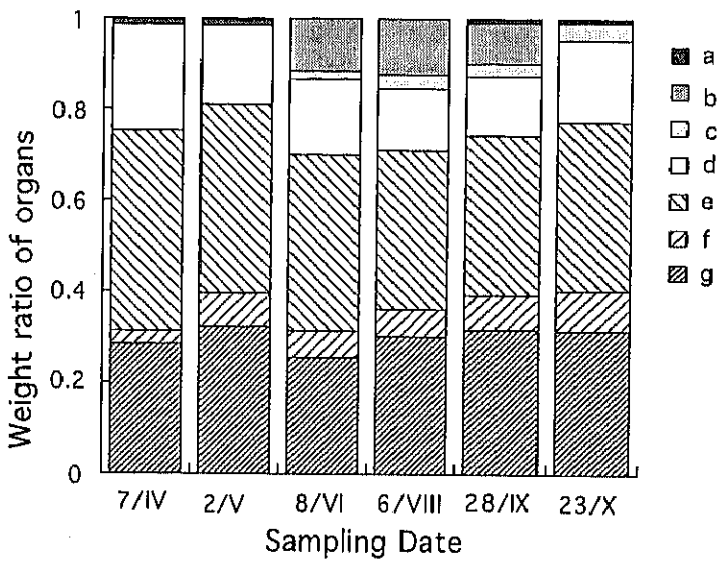

Fig. 5. Seasonal change of weight ratio of each organ for whole plant. a : bud, b : leaf, c : current branch, d : branch, e : stem, f : rootlet and g : main root.

12% until late September and then decreased to zero percent following leaf shedding. After decreasing from April to May, the *Wb*/*W* was maintained constant at 18% in average until late September. In autumn, with leaf shedding following reallocation of carbon and nitrogen from the leaves to trunk and branches, the *Wb*/*W* ratio increased to 22%. The *Wt*/*W* ratio

decreased linearly from 42% in May to 35% in August and then increased to 62% by October. The Rm/W ratio was constant at 26-30% throughout the growing season. The Rl/W ratio was low in early spring and varied by about 7.5% during the growing season.

Seasonal changes of nitrogen and carbon concentration in each organ

Carbon and nitrogen concentration (weight ratio of nitrogen and carbon for each organ) for each season is given in Table 3. Carbon concentration for each organ was constant throughout the growing season. The carbon concentration of leaf was 49% in 8th June and 51% in 28th September. Trunk and main root contained 48% and 47% carbon throughout the growing season. However, the nitrogen concentration of each organ exhibited seasonal changes. GLAVAC *et al.* (1990) reported the same trend in nitrogen concentration in a 42-year-old beech. Leaf nitrogen concentration was 2.18% just after leaf unfolding and then decreased to 1.78% by 6th August. The non-photosynthetic organs such as branches and trunk, showed different seasonal changes from that of the leaf. The nitrogen concentration of these organ decreased until 6th August and then returned by recruitment from the leaves to the initial level by 28th September. The nitrogen concentration of each organ on 6th August was 0.4% in the branches, 0.25% in trunk, 0.26% in main root and 0.67% in rootlet.

Seasonal changes of carbon and nitrogen contents

Carbon: The carbon and nitrogen content (product of organ mass and the concentration of elements of each organ) and its seasonal change in the plant are given in Table 4. The plant (237.3 g in weight and 124.1 cm in height) contained 115.2 g carbon in April and 190.2 g in September. A plant with 8,176.7 cm^2 of leaf area assimilated 75 g of carbon in a growing season. The carbon decreased by 4.9 g and 7.9 g in trunk and branches respectively, and

Table 3. Seasonal changes of mean carbon (C) and nitrogen (N) concentration (%) of the plants with standard deviation in parenthesis.

Date of harvest		Bud	Leaf	Current shoot	Branch	Trunk	Rootlet	Root
2 May	(C)	48.3(0.4)	—	—	48.1(1.4)	48.0(0.2)	50.1(0.5)	47.0(0.7)
	(N)	1.10(0.1)	—	—	0.74(0.1)	0.47(0.1)	0.93(0.1)	0.46(0.1)
	(C : N)	43.9	—	—	65.0	102.1	53.9	102.2
8 Jun.	(C)	—	49.1(1.1)	46.6(0.3)	48.6(0.4)	48.4(0.6)	50.3(0.8)	47.9(0.6)
	(N)	—	2.18(0.4)	1.34(0.1)	0.56(0.1)	0.30(0.03)	0.83(0.1)	0.30(0.1)
	(C : N)	—	22.5	34.8	86.8	161.3	60.6	159.7
6 Aug.	(C)	—	49.7(0.5)	49.4(0.6)	48.5(0.4)	48.2(0.4)	49.2(0.3)	47.0(0.6)
	(N)	—	1.78(0.3)	0.63(0.1)	0.4(0.1)	0.25(0.02)	0.67(0.1)	0.25(0.03)
	(C : N)	—	27.9	78.9	121.3	192.8	73.4	188.0
28 Sep.	(C)	49.4(0.4)	50.6(0.6)	49.3(0.6)	48.5(0.5)	48.2(0.4)	51.0(0.4)	46.7(0.6)
	(N)	1.24(0.1)	1.71(0.1)	0.60(0.04)	0.57(0.1)	0.37(0.1)	0.81(0.2)	0.37(0.2)
	(C : N)	39.8	29.6	82.1	85.1	130.2	62.9	126.2
23 Oct.	(C)	49.5(0.1)	52.0(0.2)	51.0(0.6)	48.7(0.8)	48.1(0.6)	51.0(0.3)	46.2(0.7)
	(N)	1.0(0.1)	0.78(0.1)	0.67(0.1)	0.51(0.1)	0.28(0.02)	0.68(0.1)	0.3(0.1)
	(C : N)	45.9	66.7	76.1	95.5	171.8	75.0	154.0
25 Nov.	(C)	49.2(0.2)	51.6(0.9)	50.4(0.8)	49.2(0.4)	47.9(0.6)	51.1(0.5)	47.0(0.6)
	(N)	1.0(0.1)	1.0(0.3)	0.76(0.1)	0.67(0.1)	0.4(0.1)	1.03(0.2)	0.51(0.2)
	(C : N)	49.2	51.6	66.3	73.4	119.7	49.6	92.2

increased by 5.1 g and 6.2 g in rootlet and in main root from 7th April to 2nd May (Table 4). From 2nd May to 8th June, carbon decreased by 1.3 g in the trunk and 5.6 g in the main root. During the same period, the carbon of shoots and leaves increased by 13.6 g. Furthermore, little net plant production was observed.

In the period from 8th June to 6th August, the carbon gain was 62.2 g, which was used for the forming of new organs. From 6th August to 28th September, the carbon content continued to increase in the whole plant. Leaf carbon, however, decreased by 4.4 g, which suggests a reallocation of the carbon from the leaves to branches during this period.

Nitrogen: Table 4 shows seasonal change of nitrogen allocation for each organ. In April, total nitrogen in the whole plant of 273.3 g was 1,321.7 mg. By 28th September the amount of nitrogen increased to 2,232.2 mg in the plant of 393.9 g; the difference, 910.5 mg of nitrogen, was absorbed from the soil. From 7th April to 2nd May, nitrogen in the main root and branches decreased, and increased in the trunk and rootlet. However, no net nitrogen absorption from soil to plant was observed during this period. From 2nd May to 8th June, total nitrogen of the trunk, main root and branches decreased by 354.6 mg and increased in the leaves by 606.8 mg; 171.3 mg of nitrogen was newly absorbed from soil. The plant

Table 4. Seasonal changes of carbon (C : g) and nitorogen (N : mg) contents in the plant of 124.1 cm in height 237.3 g in weight in April.

Date of harvest		Bud	Leaf	Branch	Trunk	Rootlet	Root	Whole plant
Carbon								
7 Apr.	(a)	1.6	—	27.4	51.0	3.5	31.7	115.2
2 May	(b)	1.7	—	19.5	46.1	8.6	34.9	110.8
	(b)-(a)	0.1	—	-7.9	-4.9	5.1	6.2	-4.4
8 Jun.	(c)	—	13.6	21.4	44.8	7.0	29.3	116.1
	(c)-(b)	-1.7	13.6	1.9	-1.3	-1.6	-5.6	-5.3
6 Aug.	(d)	—	22.6	30.2	62.1	10.9	52.4	178.3
	(d)-(c)	—	9.0	8.8	17.3	3.9	23.1	62.2
28 Sep.	(e)	1.4	18.2	30.6	66.4	15.5	58.2	190.2
	(e)-(d)	1.4	-4.4	0.4	4.3	4.6	5.8	11.9
Nitrogen								
7 Apr.	(a)	38.9	—	370.6	430.8	61.5	419.9	1,321.7
2 May	(b)	37.5	—	304.2	456.0	159.2	342.9	1,299.9
	(a)-(b)	-1.4	—	-66.4	25.2	97.7	-77.0	-21.8
8 Jun.	(c)	—	606.8	293.6	274.7	115.9	180.2	1,471.2
	(c)-(b)	-37.5	606.8	-10.6	-181.3	-43.3	-162.7	171.3
6 Aug.	(d)	—	812.1	281.0	327.2	148.2	289.8	1,858.4
	(d)-(c)	—	205.3	-12.6	52.5	32.3	103.6	387.2
28 Sep.	(e)	34.2	614.0	357.9	514.5	245.1	466.5	2,232.2
	(e)-(d)	34.2	-198.1	76.9	187.3	96.9	176.7	373.8

absorbed 387.2 mg of nitrogen from soil from 8th June to 6th August and was distributed to the leaves, trunk and main root. From 6th August to 28th September, 373.8 mg of nitrogen was absorbed by the plant. At the same time, nitrogen in the leaves was withdrawn to the trunk, branches and main root. The nitrogen remaining in the leaves when they shed were equivalent to 10% of total nitrogen absorbed from soil during a growing season. The nitrogen allocation in the plant during August was 44% for leaves, 15% for branches, 18% for trunk, 8% for the fine roots and 16% for main root in August. The 3% nitrogen in the buds in April was used forming leaves and current branches. During the full leaf period, 44% of total nitrogen was distributed to the leaves. After late September, a marked decline in nitrogen concentration of the leaves was observed. In May, 23% of the total nitrogen was distributed to the branches. The rate declined to 11% by August and increased again to 16% in September. Nitrogen in trunk decreased from 35% to 19% at leaf unfolding time and maintaining the rate until early August and returned to 23% in September. In early May, 26% of total nitrogen was distributed in the main root, changing to 12% in early June, after which it increased to 21% by September. Nitrogen distribution in the fine roots changed from 12% to 8% at the time of leaf unfolding and recruited 14% of total nitrogen.

Discussion and Conclusion

The results of this experiment are summarized in Table 5. The weight of nut, leaf period, weight ratio of above- and below ground parts, and trunk and branches to leaves are ecological characteristics of *Fagus crenata*. The mass of the plant (124.1 cm in height and 237.3 g in weight) increased from 237.3 g on 7th of April to 393.9 g on 28th September. The maximum assimilation occurred in the period from 8th June to 6th August (59 days). The observed time of solar radiation for the 59 days was 816.5 hr. The net carbon gain for the 816.5 hr was 62.2 g with 8,176.7 cm^2 of leaf area. The mean photosynthesis rate in this period, therefore, was about 3.4 mg $CO_2/dm^2/hr$. NOMOTO (1964) reported the maximum net photosynthetic rate of 10.2 mg $CO_2/dm^2/hr$. According to MARUYAMA (1980) and MARUYAMA and KAZAMA (1987), the same figures were 5.2 and 8.6 mg $CO_2/dm^2/hr$ in the pot-grown plants.

The equation 2 is the solution of differential equation of $(1/R)dR/dt = c(1/T)dT/dt$. This implies that the plants grow with partitioning the assimilated matter to above- and below ground parts with relative allocation rate (RAR) c. In the sapling stage of *Fagus crenata*, the c is 1.18. HASHIZUME and NOGUCHI (1977) obtained the values of c as 0.93 within the forest and 0.79 on the forest margin, respectively. Also, the plant grows with RAR of 1.07 to trunk and branches, and leaf in the same relation.

KING (1990) described that the saplings of canopy species of panamanian forest allocate biomass for efficient height growth.

After completing the leaf unfolding by early June, the plant did not form any new leaves during the growing season. Therefore, the surplus matter assimilated after early June was reserved in the non-photosynthetic organs. Before shedding the leaves 13.6% of leaf carbon

Table 5. Ecological characteristics of *Fagus crenata* in sapling stage of 124.1 cm in height and 237.3 g in weight.

Characteristics	Values
Nut weight (standard deviation) (g)	0.15(0.02)
Nut size (cm)	1.34-0.63
Days needed for leaf unfolding	16(21 May-6 Jun.)
Leaf period (days)	150(21 May-18 Oct.)
Height growth in the growing season (cm)	28.8
Weight growth in the growing season (g)	156.6
Relationship between weights of above (T : g) and below ground (R : g) parts	$R=0.77T^{1.18}$
Relationship between weights of leaves (Wl : g) and trunk and branch (Wtb : g)	$Wtb=3.75Wl^{1.07}$
Leaf area per 1 g leaves: cm^2	184.3
Leaf area of a plant: cm^2	8,176.7
Mean photosynthetic rate from 8 Jun. to 6 Aug. (mg $CO_2/dm^2/hr$)	3.4
Reallocation rate of carbon from leaves at shedding time (%)	13.6
Recollection rate of nitrogen from leaves at shedding time (%)	53.9
Nitrogen absorbed from soil during growing season (g)	0.91
Mass increment/Nitorgen absorbed (g/g)	172.1

was transferred from the leaves to the branches and trunk. The reserve substances in these organs are utilized for the construction of the following year's leaves and shoots. KANAZAWA (1981) stated that "soluble" carbohydrate were withdrawn from leaves of *Fagus crenata* seedling. The saplings also withdraw 53.9% nitrogen from leaves just before leaf shedding and stores it in the branches and trunk. Mass increment of the plant per unit nitrogen absorbed from the soil was 172.1.

A set of these ecological characteristics mentioned above may contribute to make *Fagus crenata* predominate in the climax forest. The ecological characteristics of other successional dominants such as *Quercus mongolica* ssp. *crispula*, *Betula platyphylla* var. *japonica* and *Pinus densiflora* remain to be studied to explain the mechanism of succession.

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